THE ANATOMY OF *LINDSAYA LINEARIS* AND *LINDSAYA MICROPHYLLA*.

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(Thirty-four Text-figures.)
[Read 28th October, 1925.]

Introduction.

On account of recent anatomical investigation on the rhizome of the genus *Lindsaya*, many new and interesting facts have been revealed. These facts have led to a great deal of discussion, but at present it is generally accepted that the type of stele characteristic of the genus is one which is intermediate between the protostele and the solenostele. The primitive nature of the stelar structure is of further interest since the plant presents other features which are relatively advanced.

This form of anatomy, generally known as the "Lindsaya-type", was first observed in *Davallia repens*, a form closely allied to the Lindsayas, by Trécul in 1885. Unfortunately this investigator overlooked the most interesting features. In 1902, Tansley and Lulham described this type of stele for five species of *Lindsaya*. It was these investigators who gave it a perfectly correct interpretation. Gwynne-Vaughan, in 1903, described further interesting forms in the sequence of events leading from the Lindsaya-type of stele to the solenostele. The most recent work is that of McLean Thompson, published in 1920, who describes the stele in terms of the ontogeny.

The species described in the present communication are two which are of relatively common occurrence in New South Wales, namely, *Lindsaya linearis* (Swartz.) and *Lindsaya microphylla* (Swartz.). In some instances they occur in fairly dry sandy soils associated with such types as *Schizaea bifida*. Under these conditions they show features typically associated with xerophily. In other instances they occur in fairly moist positions, when the leaves show a filmy nature. *L. linearis* particularly is often found in very swampy country.

The ferns are quite small, with creeping rhizomes which often show dichotomous branching. In *L. linearis* the fronds are from a few inches to a foot in height, the sporophylls usually taller than the ordinary leaves. The rachis is dark and shining. The pinnules are entire or nearly so, and usually distant. In *L. microphylla* the fronds are thin, with a slender, usually flexuous, rachis. The barren pinnules are lobed. In both species the sori are continuous.

The various parts of the plant were fixed in the field in a 1% chromo-acetic solution and passed in the usual manner into paraffin. Sections were then made of the various parts varying from 3μ to 12μ in thickness and stained in Flemming's triple stain, this proving very satisfactory for all parts of the plant.

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Investigation.

A. *Rhizomes.*

The rhizomes of both types are covered by a fairly extensive development of scales which become very profuse around the apex. The rhizomes show a fairly regular dichotomous branching which, although uncommon among the Polypodiaceae as a whole, has been observed in numerous species of *Lindsaya*, and seems to be a fairly constant feature of the genus. These branches bear the same structure as the main axis from which they arise.

The apices of the stems are alike in both forms and are of the general nature described for Polypodiaceous types. This is indicated in Text-fig. 1, where it will be observed that the apex consists of a small cone, slightly raised above the general level of the rhizome, and terminated by a large initial cell, tetrahedral in shape, which is deeper than broad. Segmentation takes place in the usual manner, segments being cut off parallel to the cutting faces of this cell. These segments are further divided into one inner cell and two outer cells. The latter give rise to the cortex and epidermis, the former to the vascular system of the rhizome.

Behind the apex, the cortex becomes sclerized and from the outer limits scales arise. Siliceous nodules, often irregularly shaped, occur in the cortical cells.

The vascular systems of the rhizomes of both types have been mentioned as conforming with the "Lindsaya-type" by Gwynne-Vaughan and Bower. This is further indicated in Text-figs. 2-4. These figures represent sections made from the internodes of the respective types. It will be observed that the greater part of the bundle is occupied by xylem, accompanied by xylem-parenchyma and surrounded by phloem, pericycle and endodermis. Towards the upper or dorsal surface of this solid core of xylem, a pocket of internal phloem associated with internal parenchyma occurs. The dorsal mass of xylem is very thin, forming a bridge over the internal phloem, while the ventral mass of xylem is very much thicker. The xylem tracheids are of fairly uniform size and are composed solely of scalariform elements; spiral or annular tracheids corresponding to the

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Text-figures 1-8.

1. A longitudinal section of the stem apex of *Lindsaya microphylla* showing the tetrahedral apical cell (X) and the typical segmentation. × 180.
2. Transverse sections of the vascular bundles of *L. microphylla* (2a) and *L. linearis* (2b), showing the central core of xylem (xy) with its internal phloem ($i. ph.$) surrounded by external phloem ($ex. ph.$), pericycle (p) and endodermis (en). × 40.
3. A transverse section of the dorsal portion of the vascular bundle of *L. microphylla*. $xy. p.$, xylem parenchyma; $xy.$, xylem; $i. ph.$, internal phloem; $m.$, internal parenchyma; $ex. ph.$, external phloem; $p.$, pericycle; $en.$, endodermis. × 180.
4. A transverse section of the dorsal portion of the vascular bundle of rhizome of *L. linearis*. × 180.
5. The same as the above except that a leaf trace is about to depart, forming a small dorsal projection. The break in the continuity of the dorsal arc of xylem will occur in the vicinity of x. × 100.
6. A stage further advanced in the departure of the leaf trace. The dorsal arc of xylem has broken and rotated laterally outwards. Internal and external phloem are in communication. $p. xy.$, protoxylem. × 100.
7. The gap caused in the xylem by the departure of the leaf trace has again closed. × 100.
8. A transverse section of the internal phloem showing xylem tracheid incorporated within it. × 180.
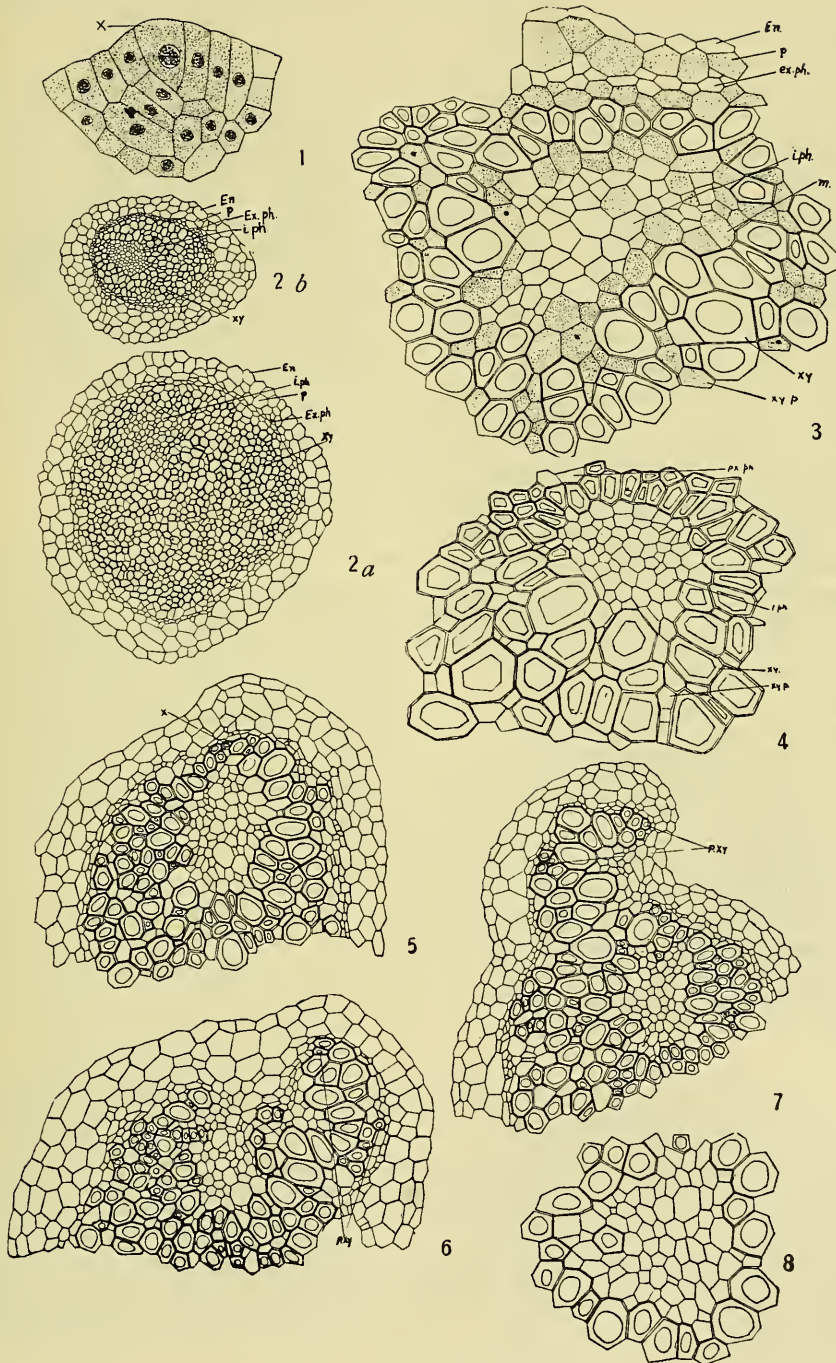
protoxylem were not observed, although a careful search was made for them. Xylem parenchyma is more abundant in the rhizome of *L. microphylla* than in that of *L. linearis.*

The "internal pocket" is composed of phloem and parenchyma. In *L. linearis,* this parenchyma consists solely of a layer of cells separating the xylem and phloem; in *L. microphylla,* the internal phloem itself has a few intermingled parenchymatous cells as well. The sieve tubes of both the internal and external phloem are of fairly uniform size, and show no differentiation into protophloem and metaphloem, protophloem elements not being present in the stem. It is interesting to note in this connection that Gwynne-Vaughan describes protophloem as being present on the outer margin of the external phloem of *Davallia repens.* The external phloem consists of one or two rows of sieve tubes surrounding the xylem and separated from it by a layer of parenchymatous cells. The pericycle is composed of large cells, two to four cell layers deep and surrounded by the characteristic endodermis. The root trace departs from the outer margin of the ventral portion of xylem directly opposite the dorsal arch and passes through the cortex with the minimum of disturbance. The leaf trace comes off as a single curved strand, in departing breaking the dorsal arch of xylem, thus placing the internal and external phloem in communication (Text-figs. 5-7).

Text-figure 5 represents a section approaching the node, and it will be observed that here the internal phloem has formed a projection resulting in a thrusting up of the dorsal arc of xylem in its vicinity. This is brought about by an increase in the amount of phloem present in the stem, causing this dorsal projection in order to accommodate the added bulk. The phloem now commences to extend laterally outwards; the strain thus set up causes a breaking at the dorsal arc at a point X (Text-fig. 5), where this dorsal projection meets the unaltered part. This break in the continuity of the dorsal xylem places the internal and external phloem in communication. There is no involution of the endodermis. The free end of the xylem then commences to rotate laterally outwards, and is closely followed by the internal phloem. Thus the internal phloem of the leaf trace is derived from the internal phloem of the bay. This condition is indicated in Text-fig. 6. A wide gap is formed in the stelar tissues as a result of the movement of the arc, and the free communication of the internal and external phloem is very pronounced at this point. It is here that protoxylem elements begin to make their appearance in the trace which had hitherto been without them. The arc of xylem now commences to raise itself from the dorsal surface of the broken stele, and deepens its concavity so as to take on a gutter-


Text-figures 9-15.

9. A longitudinal section of the apex of the petiole of *L. linearis* showing the wedge-shaped apical cell forming two rows of segments. × 200.
10. A transverse section of the petiole of *L. linearis.* × 45.
11. A transverse section of the petiole of *L. microphylla.* × 25.
12. A transverse section of the petiolar bundle of *L. microphylla* showing three protoxylem groups (p. xy.) and ⋂ shaped mass of metaxylem surrounded by phloem pericycle and endodermis. × 200.
13. A transverse section of the petiolar bundle of *L. linearis.* × 200.
14. A transverse section of the pinnule of *L. linearis* showing upper and lower epidermis with thick cuticle, stomata confined to the lower surface, and spongy mesophyll. × 110.
15. A longitudinal section of the root apex of *L. linearis* showing the pyramidal apical cell with its segmentation, and the root cap. × 200.
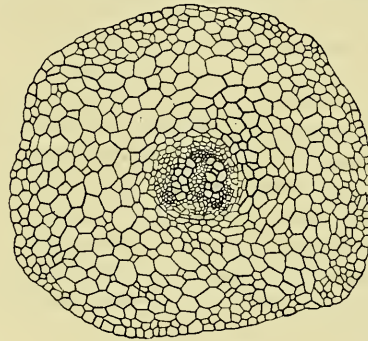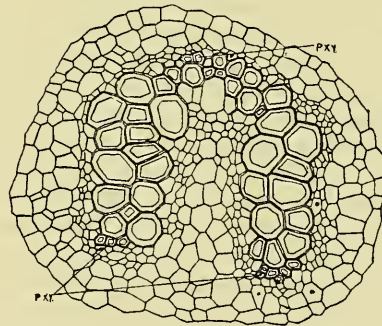
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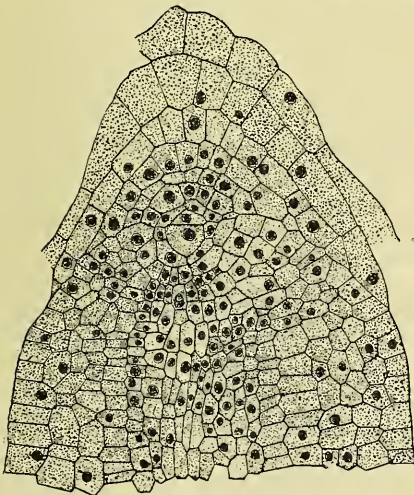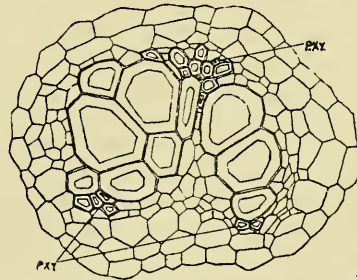
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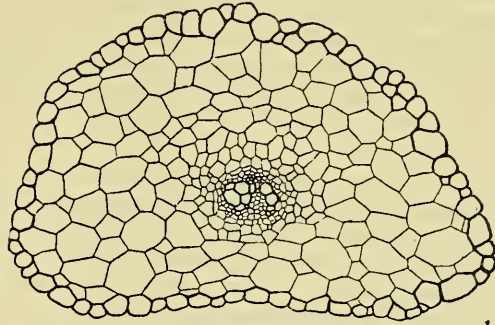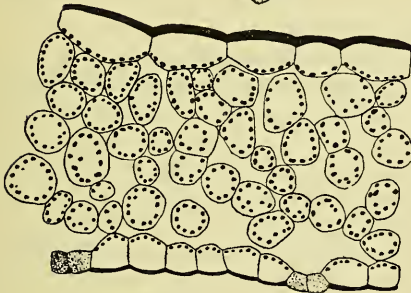
shaped form. The broken dorsal vault again becomes complete before the leaf trace is properly detached (Text-fig. 7). The arc of xylem continues to raise itself until it becomes detached from the xylem of the stem. At the same time the external phloem, pericycle and endodermis become folded in until, finally, complete separation of the two structures is brought about and the meristele of the petiole is formed, its plane of symmetry being parallel to the dorsal surface of the stele.

These facts are in very close agreement with those described by Tansley and Lulham (1902, pp. 158-9) in *L. orbiculata*, with one important difference, namely, that no internal endodermal cells appear in the internal phloem in connection with the departure of the leaf trace. These investigators have stated that "as the free end of the arc moves away from the stele the internal endodermis approaches the outer one, they touch and open, thus placing the inner strand of parenchyma which had dilated considerably into connection with the cortex". In *L. microphylla* and *L. linearis* the leaf trace, as it separates, is always limited externally by unbroken endodermis. Although not directly stated, it seems that the underlying idea of these authors is that the internal pocket arose by flow of tissue, the parenchymatous cells being derived from the cortex.

McLean Thompson (1920, p. 727), who describes the structure in terms of the ontogeny, considers that "the formation of medulla and inner phloem involves neither cortical intrusion nor tissue flow, but is the result of static intrastelar change by which also the pockets in the adult stele arise."

During the course of the investigation, the writer observed the presence of isolated tracheids in the internal phloem pockets, further indication of change of procambial destination of cells *in situ* (Text-fig. 8). This is the idea put forward by Bower.

It is generally recognized that the great interest of the "Lindsaya-type" of stele is that it appears to furnish a phylogenetic link in the sequence from the protostele to the solenostele. Gwynne-Vaughan (1903, p. 717) expresses very concisely the nature of this change: "As the leaf and the trace increased in importance relative to the stem, the phloem lying on the adaxial side of the leaf trace became extended downwards into the substance of the xylem of the protostele. Gradually reaching further down through the internode, this internally decurrent phloem at length comes into contact with that decurrent from the leaf trace below, and a continuous solid core of phloem was thus formed within the stele. Then the ground tissue lying in the adaxial concavity of the leaf trace also began to extend downwards into the stele forming at first a prolongation that ended blindly in the core of phloem but eventually it reached down from one leaf trace until it met with that decurrent from the next leaf trace above. In this manner an internal strand of ground tissue was formed which is continuous throughout the stem and the stele became a solenostele".

This mode of formation of the solenostele implies that there was present a continuous core of internal phloem before the ground tissue became decurrent at all. But, taking into consideration Boodle's (1901) description of the structure of the node of *Gleichenia flabellata*, it appears that phloem and ground tissue were decurrent together into the xylem of the protostele. It follows that the soleno-stele may have originated by either of these two methods, and does not necessarily come along one line of descent.

Another feature of interest with regard to this "Lindsaya-type" of stele is that it has frequently been described in the ontogeny of higher types of stele. Since

Lindsaya presents other features which are relatively more advanced, Bower (1918, p. 61) considers that *Lindsaya* may be held to have stood still anatomically at an early stage of the ontogeny, a fact possibly related to its restricted leaf development, while others with more ample leaf development have progressed to solenostely and other complications.

B. *Leaves.*

A two-sided wedge-shaped apical cell forming two rows of segments is the type for the leaf of both forms. This is shown in Text-fig. 9 (*L. linearis*). The outer divisions of the segments are the marginal cells which give rise to the pinnae of the leaf; the other segments are mainly formative of the petiole. As each pinna corresponds to a segment of the apical cell, it follows that they alternate on opposite sides of the rachis. The leaf first makes its appearance as a blunt conical emergence, but as the leaf grows it assumes the form of a flattened cone with a broad base, more convex on the outer side and very soon showing circinate vernation.

1. *Petiole.*—The minute anatomy of the petiole of *L. microphylla* and *L. linearis* is practically identical. The transverse section is circular to oval in outline (Text-figs. 10-11). The cortex is composed of very large, thin-walled cells, particularly large in *L. linearis*, in which intercellular spaces are absent. Two or three layers of sclerenchyma occur on the outer limits.

The centre is occupied by a single vascular strand, subrotund in outline. The petiolar bundle is concentric and contains a xylem strand, ∩-shaped in *L. microphylla* (Text-fig. 12), the arms of the ∩ being very thick, and ∧-shaped in *L. linearis* (Text-fig. 13), the bases being directed towards the apex of the stem. The metaxylem elements in *L. linearis* are few in number but very large, in some instances the arms of the ∧ being occupied by a single row of tracheids. These large tracheids have scalariform thickening laid down on their walls.

Immediately one end of the leaf trace becomes separated from the stem stele, protoxylem groups make their appearance in the bundle which had hitherto been without them; these protoxylem groups being three in number. Two are placed on the ends of the arms of the xylem, appearing when the ends become separated from the stem bundle; consequently one appears before the other. The third group is placed at the apex and its position is variable in the two species. In *L. microphylla* it was observed in all positions intermediate between endarchy and exarchy, primarily endarch but finally it forms the connection between the two arms of the ∩. In *L. linearis*, on the other hand, this third protoxylem group is always exarch, appearing in that position from the first in the leaf trace. It often, in section, has the appearance of being squeezed out by the large metaxylem elements.

The three protoxylem groups in the Polypodiaceae are considered as being primarily endarch. A somewhat similar transition of the median protoxylem group from an endarch to an exarch position was described by Marsh and confirmed by the writer (1924) in various species of *Cheilanthes.*

Here the movement of this protoxylem group may be traced at different levels of the petiole till it becomes exarch in position, and finally, in *Cheilanthes fendleri* and *Ch. tenuifolia*, becomes completely detached from the main mass of metaxylem elements, and is broken up into three or four smaller groups.

Bertrand and Cornaille (1902, p. 99) considered that the trace with three protoxylem groups resulted from the fusion of two binary chains (the latter

term being employed for the trace with two protoxylem groups) and the reduction of the median bipolar group thus formed to a minimum. Both of these forms have been derived in their turn from more complicated types.

Gwynne-Vaughan (1903, p. 722) has objected, however, that hardly any evidence can be brought forward to support this theory of reduction. The facts rather seem to the writer to present a series in the progression of the leaf trace. The movement of this median protoxylem from the endarch to the exarch position causes a break in the continuity of the metaxylem elements which appear to die out at this level. The protoxylem comes to form the only connection between two distinct metaxylem masses, and by the splitting of this protoxylem group in this position into two, there would be formed two xylem masses, each with two endarch protoxylem groups. Later, the phloem, pericycle and endodermis might follow this; thus two bundles would be present in the petiole. These in their turn, by further division, would give rise to more complicated types.

The phloem of the bundle in the forms under consideration is separated from the xylem by a single layer of parenchyma. It consists of two rows of sieve tubes which surround the xylem without any interruption in their continuity. The sieve tubes are of uniform size and represent the metaphloem. Protophloem is not represented in either type. This is surrounded by the pericycle which is several layers deep. The whole is encircled by the endodermis. When the


Text-figs. 16-34.

16. A longitudinal section of the root apex in *Lindsaya microphylla*. × 200.
17. A transverse section of the root apex of *L. linearis* showing the apical cell and its segmentations. × 200.
18. A transverse section of the root of *L. linearis*. × 45.
19. A transverse section of the root bundle of *L. linearis* showing its diarch nature. The xylem is surrounded by phloem, pericycle and endodermis. × 200.
20. A transverse section of the root bundle of *Lindsaya microphylla*. × 200.
21. A cortical cell of the root of *L. linearis*, showing the septate branching and multi-nucleate nature of the fungus infecting it. The nucleus of the host is well developed. × 450.
22. A longitudinal section of the pinnule of *L. microphylla* in the region of the sorus showing the nature of the indusium and the receptacle deflected towards the lower surface. × 45.
23. A longitudinal section of the young sporangium of *L. microphylla* showing the basal cell and the sporangial cell proper. × 200.
24. A longitudinal section of a later stage in the development showing the central cell which has cut off the wall cells and the three rows of cells in the stalk. × 200.
25. The central cell is here cutting off the tapetum. × 200.
26. At this stage of development the archeosporium has divided into four cells, the spore mother cells. × 200.
27. A longitudinal section of the sporangium showing the disintegrated tapetal cells. The spore mother cells have enlarged, separated and become rounded. × 200.
28. A transverse section of a spore mother cell showing the chromosomes after synapsis. × 450.
29. A section of a spindle formed during the division of the spore mother nucleus, showing three of the four poles which are sometimes formed. × 450.
30. A mitotic spindle formed during the nuclear division of a cell of the petiole tip of *L. microphylla,* showing the large number of chromosomes present. × 450.
31. A mitotic spindle formed during the nuclear division of the spore mother cell of *L. microphylla* showing the reduced number of chromosomes. × 450.
32. This indicates the typical arrangement of the spores formed from the division of the spore mother cells of *L. microphylla*. × 200.
33. The spores of *L. linearis.* × 200.
34. The spores of *L. microphylla*. × 200.
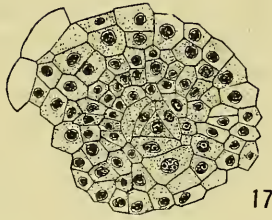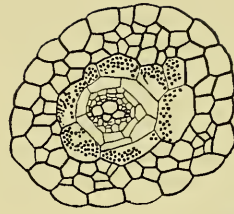
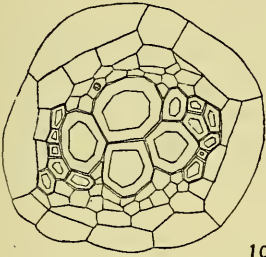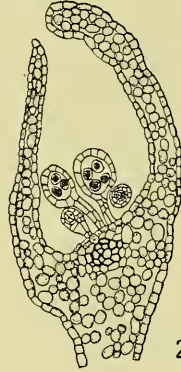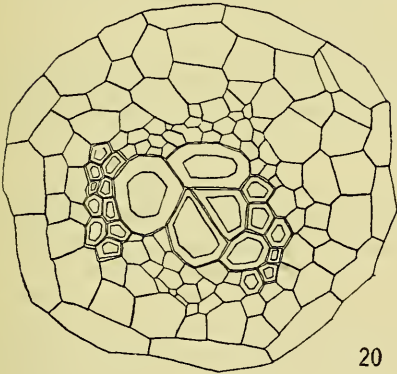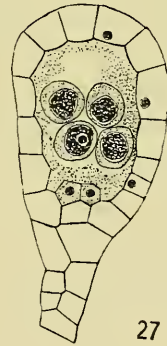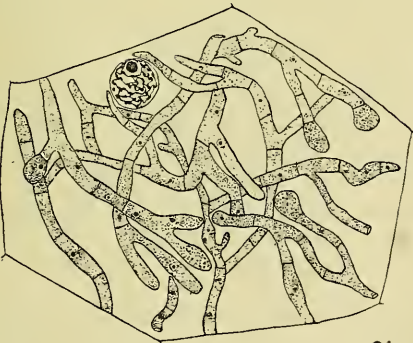petiole reaches the level of the pinnae, branches are given off from the petiolar bundle, which constitute the vascular supply to the rachis.

It is perhaps worthy of note that very occasionally the writer has observed, in *L. microphylla*, the petiole itself branching dichotomously.

2. *Pinnules.*—In both types the barren pinnules are frequently lobed. The veins show a very regular dichotomous branching. The pinnules of *L. linearis* are of a much deeper green colour than those of *L. microphylla*.

The cells of the upper and lower epidermis are large and have a very thick cuticle. The stomata are confined to the lower surface of the leaf and open into large air cavities (Text-fig. 14). The pinnule in both types is characterized by the absence of palisade tissue, the whole of the tissue between the two epidermes being composed of parenchyma with large intercellular spaces. The cells of this mesophyll contain very large chloroplasts which are distributed fairly evenly around the margins of their walls. The absence of palisade tissue and the arrangement of the chloroplasts probably bear relation to the light intensity. The vascular bundle of the pinnule is usually collateral. It is surrounded by endodermis, composed of large thin-walled cells. This encloses a mass of tracheids representing the xylem surrounded by parenchyma with a few sieve tubes.

C. *Roots.*

The roots arise in connection with the bases of the leaves. The primary roots branch profusely; the branches arise in two lines, corresponding to protoxylem groups in the vascular bundle of the primary root.

Text-figures 15, 16, 17 indicate that the apex of the root of both ferns is characterized by the presence of a three-sided pyramidal apical cell, from the sides of which segments are cut off in regular succession. The formation of the body of the root and the root cap may be traced to definite segments of the apical cell.

The cortex is two or three cell layers deep and very quickly becomes sclerized (Text-fig. 18). The vascular bundle of the root is surrounded by the endodermis which is not always to be observed in the older portions (Text-figs. 19-20). The root is diarch; xylem is composed of protoxylem and metaxylem; the elements of the latter are large and have scalariform thickening laid down on their walls. The phloem is well developed and is separated from the xylem by a layer of parenchyma. It does not, however, extend round beyond the protoxylem groups where xylem and pericycle are in contact. There is a multilayered pericycle, the cells of which are large and often have a great deal of starch stored within them.

A curious feature of the root in both forms is that fungal hyphae appear in the cortical cells a little behind the apex (Text-fig. 21), indicating the presence of mycorhiza in the roots. The cortical cells in which the fungus is present are large and have thin walls. Fungal hyphae were observed passing through the walls from one cell to another. The fungus is a branching, septate, multinucleate form. The ends of the branches are often swollen. Fungal sporangia were also observed in the cells. No root nodules are visible externally, so that the presence of the fungus evidently does not stimulate the plant to form new tissues. Symbiosis was observed to be a constant feature in the root, no matter from what situation the plant was collected.

Mycorhiza have been recorded from other parts of the Pteridophyta. Laing (1899) describes an endophytic fungus present in the prothallus of *Lycopodium clavatum*. In 1917, Lawson found the same in the prothalli of *Tmesipteris* and *Psilotum*.

D. *Sorus.*

The sporophylls are usually not lobed, but are often rolled inwards, affording protection for the sori. The latter are borne on the ends of the veins which are linked together distally to form a continuous vascular commissure. The sporangia have followed this extension of the vascular supply and thus the fusion sorus has arisen. This is characteristic of the genus.

The tracheids composing the vascular commissure to the sporangia are of a different nature from those present in the ordinary veins of the leaf. Those of the vascular commissure are shorter, broader and of the nature of storage tracheids. This has also been described by Bower (1914) as occurring in connection with the fusion sorus of the Blechnum type.

The nature of the sorus, indusium and receptacle, and their early development in *Lindsaya linearis* have been carefully investigated and described by Bower (1918, pp. 14-15). The marginal cells, as in *Dicksonia*, become the apex of the receptacle by segmentation; the two indusial flaps originate intramarginally, as in *Dicksonia*, differing in bulk, the inner (abaxial) being thinner while the receptacle is deflected towards the lower surface. The sporangia at first show a gradate sequence, but later this is not strictly maintained, and young sporangia become interpolated between the older, leading to the typical mixed condition. These facts are also true for *L. microphylla*, as indicated in Text-fig. 22.

The sporangia develop in the manner typical for Leptosporangiate Ferns. One of the cells forming the wall of the receptacle enlarges and is cut off by a transverse wall into a basal cell which undergoes no further division, and an upper cell which forms the sporangium proper (Text-fig. 23). The upper cell undergoes divisions which result in the formation of a pyramidal apical cell from which various segments are cut off, giving rise to the three rows of cells seen in the stalk. These undergo no further longitudinal divisions. The upper part of the sporangium enlarges and a periclinal wall is formed in the apical cell. Thus the wall cells are cut off, and remain permanently one layer thick (Text-fig. 24).

The central cell of the sporangium cuts off a single layered tapetum by further division (Text-fig. 25), and this, later by a further periclinal division, becomes double.

The archeosporium develops up to the quadrant stage (Text-fig. 26), but often undergoes no further development in *L. microphylla*, so that there are usually only four spore mother cells, although occasionally six are present. In *L. linearis*, however, there are frequently eight spore mother cells developed.

As the subsequent development is the same in both types, in order to avoid unnecessary duplication, the following description and text-figures will be taken from *L. microphylla*. As soon as the spore mother cells are formed, the tapetum begins to disintegrate, the spore mother cells separate, and become rounded and very much larger (Text-fig. 27). The nuclei of these cells enlarge considerably until they become almost as large as the cell itself, leaving a very thin selvage of protoplasm around the wall. The linin network of the nucleus at this time becomes very distinct.

After the complete disintegration of the tapetal cells, the nucleus prepares for division. It undergoes the typical stages associated with reduction division, chromosomes are formed (Text-fig. 28) and finally a spindle is produced. The chromosomes pass to the poles of the spindle, and two nuclei are produced. These nuclei undergo another division differing from the former in that it is homotypic

in nature. Thus four nuclei, and finally four spores are produced from each spore mother cell, the tetrad having the typical arrangement indicated in Text-figure 32.

It frequently happens that the second division occurs so rapidly after the first that a spindle with four poles is produced (Text-fig. 29). The number of chromosomes present is the same as that found associated with the second division. This is frequently found in the division of the spore mother cell of the Filicales.

Text-figure 30 represents a mitotic spindle observed in a petiole tip. Here the number of chromosomes present was counted as being from 32 to 40. In the second division of the spore mother nucleus only 16 chromosomes are present (Text-fig. 31).

The wall becomes organized into various parts (annulus, etc.). This has been described and figured by Bower for *L. linearis* (1918, p. 16, fig. 14).

After the division of the spore mother cell, the four spores are enclosed within the mother membrane. This disintegrates and the spores become separated, their walls undergoing various modifications. The outer wall becomes very thick, and spiny. The form of the spore in both cases is tetrahedral (Text-figs. 33-34).

The number of spores present in *L. microphylla*, by actual count, was 16-24, in *L. linearis* 24-32. The latter confirms the estimate made by Bower.

Bower (1918) considers that the marginal origin of the receptacle in such types as *Lindsaya* and *Dicksonia*, etc., where it becomes downward-directed as development proceeds, illustrates how the initial steps in the modification to a superficial sorus may be actually observed in the ontogeny of the typical Marginales.

Conclusion.

The view which is universally supported at the present day, is that *Lindsaya* is a genus anatomically primitive, but possessing other characters which are more advanced.

Its affinities, as determined by anatomical structure and soral character, are with the Davallieae. The soral characters also indicate relationship with the Dicksonieae, except that as the sorus becomes older it assumes a "mixed" character. Thus the sorus is more advanced than that of the Dicksonieae, although the anatomical structure is very much more primitive. In respect to its anatomical structure, then, *Lindsaya* takes a lower place than any of the Dicksonoid series.

The mature stelar structure is regarded as furnishing a phylogenetic link between the protostele and the solenostele. These are regarded as primitive types of vascular arrangement in the Polypodiaceae. Gwynne-Vaughan (1903, p. 732) remarks that these primitive characters do not run parallel with Bower's division of the order into Gradatae and Mixtae.

Bower, however, supports the view that there are several lines of descent among the Polypodiaceae alone, and a primitive type of vascular arrangement might occur in the primitive members of each line of descent. He considers that in *Lindsaya* no structural advance was made to complete solenostely, owing to the restricted size of the species of the genus which made distension of the stele unnecessary.

It seems that the convergence of evidence from many forms, indicates that anatomical structure and soral characters have not necessarily advanced together in the progressive development of the Filicales, that one or other might have advanced while the other remained stationary; that is, these characters have taken quite independent courses of evolution. Factors influencing one have not necessarily made themselves felt upon the other.

Since the structure of the rhizome of *Lindsaya* is constant in so many species, it has been suggested that it forms a good generic character.

Summary.

1. Apex of the stem in both types is occupied by a tetrahedral apical cell.
2. The stem anatomy of *Lindsaya linearis* and *L. microphylla* coincides with the "Lindsaya-type". The "internal pocket" of phloem is due to change in procambial destination of cells.
3. The leaf trace departs as a single strand from the dorsal arch in much the same manner as described by Tansley and Lulham, except that no internal endodermis appears.
4. Apices of the leaves are occupied by a two-sided wedge-shaped apical cell forming two rows of segments.
5. Petiolar bundle forms a single strand containing three protoxylem groups, two of which are endarch in position, the third (medium) group in *L. linearis* exarch, but in *L. microphylla* occupying positions intermediate between endarchy and exarchy.
6. Stomata are confined to the lower surface of the pinnule. Cuticle thick. No palisade tissue present.
7. Apices of root occupied by a three-sided apical cell.
8. Roots are diarch.
9. Symbiosis occurs in the roots of both forms, fungal hyphae causing the infection being septate and branching and multinucleate.
10. Sorus is marginal in origin; true indusium is present; sorus is mixed in character.
11. Tracheids composing the vascular commissures are of a different nature from those of the ordinary veins of the pinnule.
12. In *L. microphylla*, 4-6 spore mother cells are formed, in *L. linearis*, usually 8.
13. Sorus of *Lindsaya* indicates how the initial steps in the ontogeny of the superfilicales may have occurred.
14. Nearest affinities of the Lindsayas are the Davallieae.

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